Foot sole and ankle muscle inputs contribute jointly to human erect posture regulation

Anne Kavounoudias, Régine Roll and Jean-Pierre Roll

Laboratoire de Neurobiologie Humaine, UMR 6562, Université de Provence/CNRS, Marseille, France

1. In order to assess the relative contribution and the interactions of the plantar cutaneous and muscle proprioceptive feedback in controlling human erect posture, single or combined vibratory stimuli were applied to the forefoot areas and to the tendons of the tibialis anterior muscles of nine standing subjects using various vibration frequency patterns (ranging from 20 to 80 Hz).

2. The variations in the centre of foot pressure, ankle angle and the EMG activities of the soleus and tibialis anterior muscles of each subject were recorded and analysed.

3. Separate stimulation of the plantar forefoot zones or the tibialis anterior muscles always resulted in whole-body tilts oppositely directed backwards and forwards, respectively, the amplitude of which was proportional to the vibration frequency. EMG activity of ankle muscles also varied according to the direction of the postural responses. However, the same vibration frequency did not elicit equivalent postural responses: in the low frequency range, tactile stimulation induced stronger postural effects than proprioceptive stimulation, and the converse was the case for the higher frequency range.

4. Under sensory conflict conditions, i.e. foot sole–flexor ankle muscle co-stimulation, the direction of the body tilts also varied according to the difference and the absolute levels of the vibration frequencies. In all cases, the resulting postural shifts always corresponded to the theoretical sum of the isolated effects observed upon vibrating each of these two sensory channels.

5. We proposed that tactile and proprioceptive information from the foot soles and flexor ankle muscles might be co-processed following a vector addition mode to subserve the maintenance of erect stance in a complementary way.

It is now generally accepted that human standing posture is maintained through a central postural programme assisted by various types of sensory feedback of mainly labyrinthine, visual, muscular and cutaneous origin that together contribute to postural stabilisation as well as being the basis of a body posture representation (Gurfinkel *et al.* 1988; Horak & Macpherson, 1996; Mergner & Rosemeir, 1998).

Motor reactions are well known to occur in response to experimental manipulation of each of these sensory modalities. In particular, postural responses are induced by electrical stimulation of the labyrinth (Lund & Broberg, 1983; Fitzpatrick *et al.* 1994; Day *et al.* 1997), vibration of ankle muscle groups (Eklund, 1972; Roll & Roll, 1988; Kavounoudias *et al.* 1999*a*), vibration of the foot soles (Kavounoudias *et al.* 1998), or exposure to moving visual scenes (Dichgans *et al.* 1975; Lestienne *et al.* 1977; Bronstein & Buckwell, 1997).

However, signals coming from these multiple sensory sources co-vary with every postural change. The question thus arises as to whether the partial redundancy of sensory information subserves some functional purpose for postural equilibrium. This might firstly explain the fact that postural balance is not systematically impaired after the definitive loss or the transient suppression of one sensory channel (Black *et al.* 1983; Diener & Dichgans, 1988; Horak *et al.* 1990). Secondly, the comparison of the various convergent inputs could be necessary to properly assess the body configuration and its current changes (Horak & Macpherson, 1996; Mergner & Rosemeier, 1998). Depending on both their location within the body and their selectivity, the different kinds of receptor probably provide the brain with complementary sensory information. For example, a proprioceptive signal indicating that the ankle muscle has been lengthened, may result from either a whole-body or a supporting surface displacement. Therefore, to elaborate appropriate

postural adjustments, the CNS might compare the sensory information from the various sources. Evidence for an interaction between information from multiple sensory sources also comes from numerous studies showing, for instance, that the direction of the postural responses induced by either visual (Wosley *et al.* 1996) or vestibular (Lund & Broberg, 1983; Ivanenko *et al.* 1999) stimulation varies according to the orientation of the eyes, the head and/or the trunk. These data lead to the conclusion that the muscular proprioceptive signals indicating the relative position of the upper body segments are jointly processed with vestibular and visual cues to organise appropriate posture.

A question remains, however, regarding the rules governing the perceptual and sensorimotor integration of different sensory information. One hypothesis is that this integrative processing follows linear summation rules because additive perceptual (Karnath *et al.* 1994) or motor effects (Hlavacka *et al.* 1995, 1996) were observed upon simultaneous stimulation of the vestibular and muscular (ankle or neck) sensory channels of standing subjects. Nevertheless, Horak & Macpherson (1996) argue that the relative 'weights' of the various sensory inputs cannot be equivalent and are permanently updated depending on a whole range of different contextual factors. For instance, by giving different instructions or modifying the postural or environmental context of the subjects, it has been demonstrated that the same sensory stimulation can induce different perceptive or motor responses, involving either the whole body or only a single body segment (Lackner & Levine, 1979; Roll *et al.* 1986; Quoniam *et al.* 1990).

In order to better understand the mechanisms underlying the integration of multisensory information for upright stance control, the present study examined the interactions between two particular modalities that are heavily involved in stance control: muscle proprioception and tactile afferents from the foot soles. Because every whole-body tilt simultaneously modifies the plantar pressure distribution under the soles and causes changes in the length of various ankle muscles, we attempted to co-activate the cutaneous and muscular mechano-receptors in these body zones. To investigate the relative contribution of these two modalities, we simulated a sensory conflict by co-vibrating the forefoot zones of both soles and the tendons of the two tibialis anterior muscles of standing subjects at different frequencies (from 20 to 80 Hz) and we tested the hypothesis of an additive effect of these frequency-patterned co-stimulations. Mechanical vibration was used as a common tool since it has been clearly demonstrated that, depending on the stimulated body site, it was able to induce oriented postural responses from mainly muscle proprioceptive or tactile origin (Eklund, 1972; Roll & Roll, 1988; Kavounoudias *et al.* 1998, 1999*a*).

METHODS

Subjects

Nine healthy adults (4 men and 5 women; age range, 24–52 years) gave informed consent to participate in this study as required by the Declaration of Helsinki (1964). The experiment was approved by the local Ethics Committee.

Stimulus

Proprioceptive stimulation was delivered by two mechanical vibrators, which consisted of biaxial DC motors equipped with small eccentric masses. They were attached to the subject's ankle by elastic bands.

Two electromagnetic vibrators (Ling Dynamic Systems, type 201) driven by rectangular electrical pulses (5 ms) coupled to power amplifiers were used for the tactile stimulation of the region of the five metatarsal heads of the soles. The two vibrator probes were of elliptical shape (30 and 75 mm of the axis lengths) to overlap the whole area. The amplitude of the vibrations (0.2–0.5 mm) was controlled by a photocell system mounted in the vibrator probes. The vibrators were fixed independently on the ground under an elevated rest so that each probe passed through a hole in the foot rest. In addition, the height of each vibrator could be precisely adjusted until the probes were flush with the subject's soles, so that the standing subject perceived only a tactile superficial sensation (for more details, see Kavounoudias *et al.* 1998).

The frequencies of both proprioceptive and tactile vibrations, which were always constant during the experimental sequence, varied (20, 40, 60 or 80 Hz) depending on the stimulation conditions. Under all co-stimulation conditions, the vibration onsets were synchronised and the stimulation always lasted for 3 s.

Procedure

Subjects were asked to stand barefoot on the foot rest with their hands at their sides, and their eyes closed. They were instructed to relax and not to resist any vibration-induced body tilts. They were promised that, if need be, the experimenter would prevent them from falling.

The two tibialis anterior muscles and forefoot zones of both soles were stimulated either separately or simultaneously using four different vibration frequencies (20, 40, 60 or 80 Hz). Twenty five combinations of stimulation were randomly tested, including the control condition, in which no vibration was applied. Under eight separate stimulation conditions, vibration was applied either to the two tibialis anterior muscles or to the two forefoot zones of the soles at each of the four frequencies. Under sixteen combined stimulation conditions, the ankle muscles and plantar zones were co-stimulated either at the same ($\Delta 0$) or at different ($\Delta 20$, $\Delta 40$, or $\Delta 60$) vibration frequencies. These latter conditions included six $\Delta 20$ conditions under which a 20 Hz-frequency difference in favour of either the proprioceptive ($\Delta 20_P$) or tactile ($\Delta 20_T$) stimulation was applied; four $\Delta 40$ conditions consisting of simultaneous vibration of the ankle muscles with 40 Hz-greater ($\Delta 40_P$) or 40 Hz-smaller ($\Delta 40_T$) frequency than that of the plantar zones; and two $\Delta 60$ conditions consisting of vibration of the ankle muscles and the plantar zones at 80 and 20 Hz ($\Delta 60_P$), or 20 and 80 Hz ($\Delta 60_T$), respectively.

Data recording

Ankle angle variations in the sagittal plane were derived from a linear potentiometer fixed on the foot support. Its axis, specifically aligned to the external malleolus of each subject's right ankle, was attached to the leg with an elastic band. The 90 deg position of the ankle joint was taken as the reference position.

Antero-posterior (Y) and lateral (X) displacements of the centre of pressure (CoP) exerted by the subject's feet were recorded by four strain gauges in the force platform disposed under the supporting elevated foot rest on which subjects stood.

EMG activities of the right tibialis anterior and right soleus muscles were recorded using two pairs of surface electrodes applied on the upper third of the tibialis anterior and on the lower third of the soleus muscle, respectively. The EMG signals were filtered with a bandwidth of 100–1000 Hz and full-wave rectified.

The sampling rate was 1 kHz during a period of 5 s including 500 ms before the vibration onset and 1.5 s after the vibration was stopped. Under each stimulation condition, 10 automatically averaged trials were run.

Data analysis

To compare the responses between the subjects, all individual data signals were normalised to the mean initial level recorded during the 500 ms prior to the stimulus. Then they were analysed during the first 3 s of recording, i.e. before the response reached a magnitude at which it was necessary for the experimenter to prevent the subject from falling.

The latency of the whole-body sways was considered as being equivalent to the onset of the ankle angle deviations from the vertical because the body always oscillated in the sagittal plane as an 'inverted pendulum' around the ankle joint. The latencies of the ankle angle deviations like those of the Y CoP displacements and the EMG responses were automatically determined at ±2 standard deviations above the mean prestimulus level. The amplitude of the postural responses was assessed by the position of the Y CoP after 2.5 s of vibration.

Under all the stimulation conditions, the EMG responses in the two antagonist ankle muscles were always oppositely directed within a comparable range in amplitude. Therefore, following the method of Fitzpatrick *et al.* (1994), the soleus EMG recordings of each subject were subtracted from those of the tibialis anterior muscle to compare the latency and the orientation of the motor activity changes in this pair of muscles with those of the postural responses.

Under the isolated stimulation conditions, in which ankle muscles or plantar zones were stimulated separately, we tested the linearity of the amplitude of the postural responses with respect to the vibration frequency (linearity test). Under the different co-stimulation conditions, the influence of the various frequency patterns on the amplitude of the postural responses was tested using separate one-way ANOVAs. Moreover, the hypothesis of additive postural effects induced by the different combined proprioceptive and tactile stimulations was tested. Using Student's paired t tests, the mean experimental amplitude of the Y CoP displacements induced by each co-vibration condition was compared to the theoretical value resulting from the sum of each subject's isolated responses obtained under the two corresponding separate stimulations.

RESULTS

Postural effects of separate proprioceptive and tactile stimulations

Whatever the frequency, tendon vibration of the two tibialis anterior muscles always gave rise to whole-body tilts directed forwards whereas backward body tilts were induced upon vibrating only the forefoot zones of both soles (Fig. 1). With proprioceptive and tactile stimulation, the vibration-induced mechanical events and the

associated EMG activities were very similar except for the fact that they were always of opposite polarity.

When vibration was applied to the plantar forefoot zones, the soleus EMG activity first increased while the EMG activity of the tibialis anterior muscle remained at its basal level (Fig. 2*A*). Then this EMG pattern was reversed: as long as the body was tilting backwards, the EMG activity progressively increased in the tibialis anterior and decreased in the soleus muscles.

Three EMG patterns could be observed in different subjects with ankle flexor stimulation: (1) an increase in the tibialis anterior activity whilst the soleus activity was stable, (2) a decrease in the soleus activity whilst the tibialis anterior remained silent, (3) a concomitant increase in the tibialis anterior and decrease in the soleus muscle activities (Fig. 2*B*). These patterns did not depend
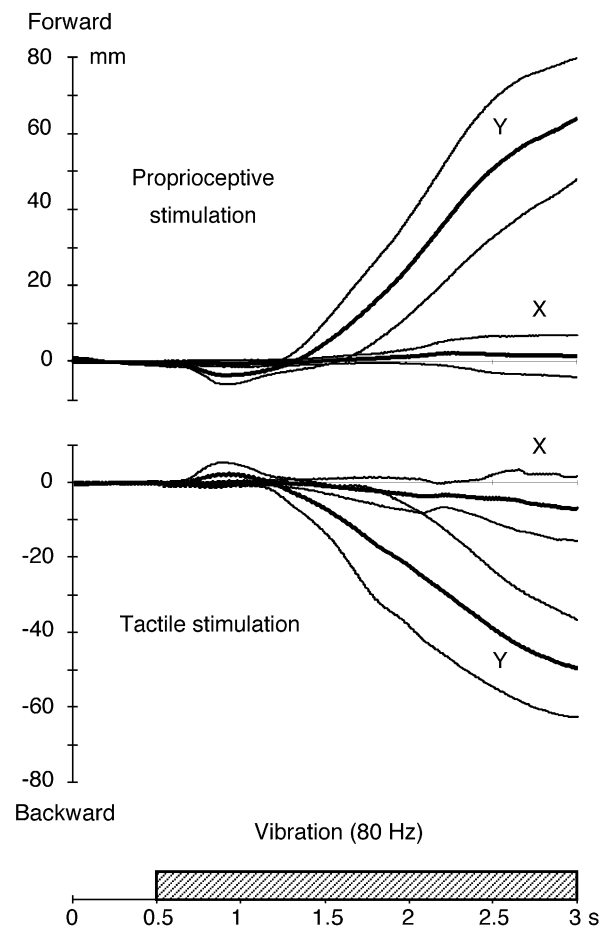

Figure 1. Typical forward and backward postural responses induced by stimulating separately the tibialis anterior muscles (top) or the forefoot zones of both soles (bottom)

Traces show the mean displacements (thick lines) and the standard deviations (thin lines) of the CoP in the antero-posterior (Y) and lateral (X) planes after 2.5 s of vibration at 80 Hz.

Table 1. Mean latencies ± s.D. (ms) of motor responses induced under all separate tactile and proprioceptive stimulations

	EMG responses	Y CoP shift	Ankle angle deviation
Forefoot zones	119 ± 28	251 ± 111	434 ± 170
Tibialis anterior	166 ± 86	286 ± 215	612 ± 291

on the vibration frequency tested. The mean latencies, which are reported in Table 1, show that for all the proprioceptive stimulation conditions, ankle muscle responses appeared significantly later than those observed upon stimulating the foot soles ($F_{1,8} = 6.3$, $P < 0.05$). Then, as soon as the body tilted forwards, a strong increase in the soleus activity occurred together with a decrease in the tibialis anterior activity to counteract the body tilt.

As clearly shown in Fig. 2A and B, the initial EMG responses in the ankle muscles were followed by an early small Y CoP shift whose direction was opposite to the subsequent body tilt. Under all the isolated stimulation conditions, these early CoP shifts always occurred before any movement at the ankle joint was detected (Table 1).

Finally, the mean latency of the ankle angle deviations was also significantly higher following proprioceptive rather than tactile stimulation ($F_{1,8} = 22.2$, $P < 0.001$; Table 1).

On the other hand, postural responses of both tactile and proprioceptive origin were found to be frequency dependent. Separate stimulation of ankle muscles or plantar zones resulted in postural responses whose amplitude was in both cases proportional to the vibration frequency used ($F_{1,8} = 44.9$, $P < 0.0005$ and $F_{1,8} = 8.5$, $P < 0.05$, respectively; Fig. 3).
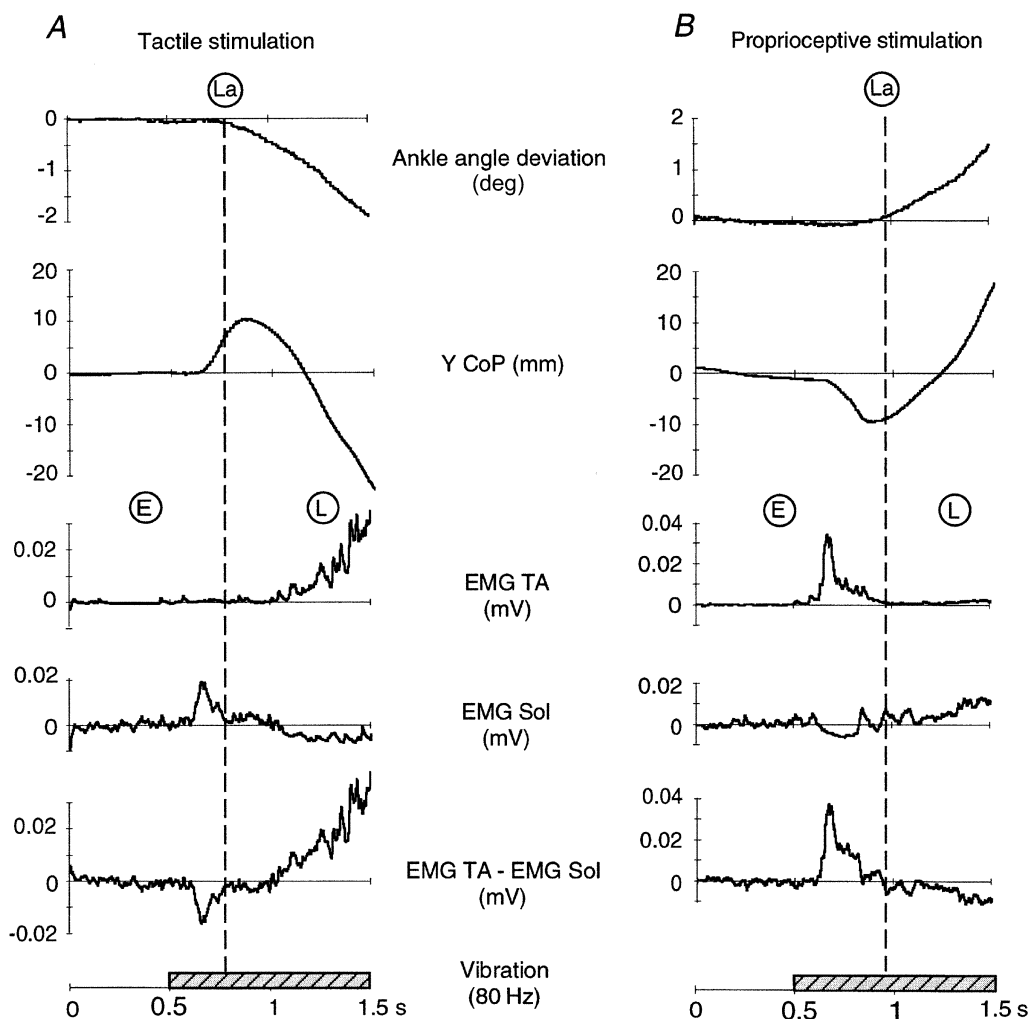

Figure 2. Mechanical and EMG changes recorded for one subject in response to tactile (A) or proprioceptive (B) stimulation at 80 Hz

La, latency of the whole-body tilt; E, early EMG responses preceding any body displacement; L, late EMG responses developed after the onset of the whole-body tilt. Note that data recordings correspond to the first 500 ms previbration and 1 s vibration to detail the initial events. TA, tibialis anterior; Sol, soleus.

However, for the same vibration frequency, the postural responses induced by proprioceptive and tactile stimulation differed quantitatively. In the case of low frequencies, i.e. 20 or 40 Hz, the postural effects observed upon tactile stimulation were significantly greater than those induced by proprioceptive stimulation ($F_{1,8} = 19.2$, $P < 0.0025$ and $F_{1,8} = 15.74$, $P < 0.05$, for 20 or 40 Hz, respectively). The mean amplitudes of the Y CoP displacements no longer differed significantly at around 60 Hz ($F_{1,8} = 0.07$, $P > 0.5$). Conversely, with a higher frequency of stimulation (80 Hz), the postural responses tended to be on average greater after proprioceptive than tactile stimulation ($F_{1,8} = 3.59$, $P < 0.2$).

All in all, stimulating only the tibialis anterior muscles or the plantar forefoot zones resulted in specific EMG activities followed by oriented whole-body tilts, whose direction was always opposite and whose amplitude varied linearly with the vibration frequency. Nevertheless, at low vibration frequencies, tactile stimulation gave rise to greater postural responses than proprioceptive stimulation, and the converse was true at higher vibration frequencies.

Postural effects of proprioceptive and tactile co-stimulations at the same frequency (Δ0 condition)

As expected from the above data, when the tibialis anterior muscles and the plantar forefoot zones were stimulated simultaneously at the same frequency, the direction of the postural responses depended on the vibration frequency range: on average subjects tilted backwards at 20 or 40 Hz, whereas on average they tilted forwards at 60 and 80 Hz (Fig. 4, □).

Given that the responses were consistent with those of the isolated stimulations of each sensory channel, we tested the hypothesis of an additive effect by calculating, for all frequencies, the theoretical sum of each subject's Y CoP deviations recorded after separate proprioceptive and tactile vibrations (Fig. 4, ■). The results show that whatever the frequency used, no significant differences were found between the theoretical values and the experimental ones (Student's paired t tests, $P > 0.1$).

Postural effects of proprioceptive and tactile co-stimulations at different frequencies (Δ20, Δ40 and Δ60 P and T conditions)

As shown in Fig. 5, simultaneous vibration of the tibialis anterior muscles and the forefoot zones of the soles at different frequencies resulted in postural responses whose direction depended on which sensory channel was stimulated at the higher frequency: when the difference in frequency was in favour of tactile stimulation (Δ20$_T$, Δ40$_T$ and Δ60$_T$ conditions), the whole-body tilts were on average directed backwards; conversely, they were directed forwards when ankle muscles were stimulated at the higher frequency (Δ20$_P$, Δ40$_P$ and Δ60$_P$ conditions).

Moreover, whatever the predominant sensory input, the amplitude of the postural responses increased as the frequency difference increased. The backward Y CoP displacements were significantly greater when the frequency difference in favour of the forefoot zones increased from 20 to 60 Hz ($F_{2,16} = 16.2$, $P < 0.0005$). The same was true when the frequency difference increased in favour of the ankle muscle stimulation ($F_{2,16} = 12.65$, $P < 0.001$).

In addition, we compared, for frequency differences of the same magnitude, the postural responses induced with all the frequency combinations. For instance, under the three combined conditions where the forefoot zones of the soles were stimulated 20 Hz more than the tibialis anterior muscles (Δ20$_T$), the mean postural responses were in all cases directed backwards but their amplitudes differed significantly according to the frequencies applied ($F_{2,16} = 6.4$, $P < 0.02$). In this case, the greater mean Y CoP shift corresponded to the co-stimulation condition where 40 and 20 Hz vibration frequencies were
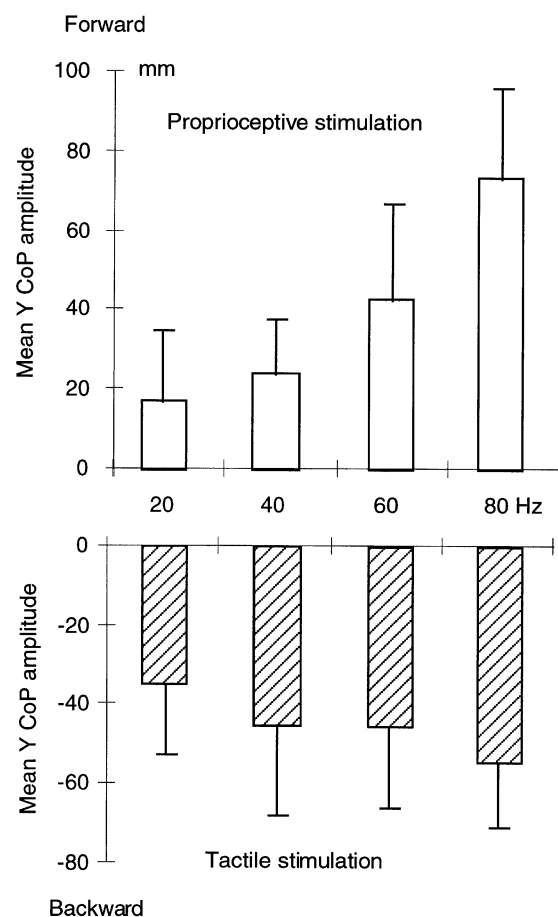

Figure 3. Mean amplitudes of the forward and backward Y CoP displacements induced by isolated proprioceptive (top) or tactile (bottom) stimulation according to the vibration frequency applied
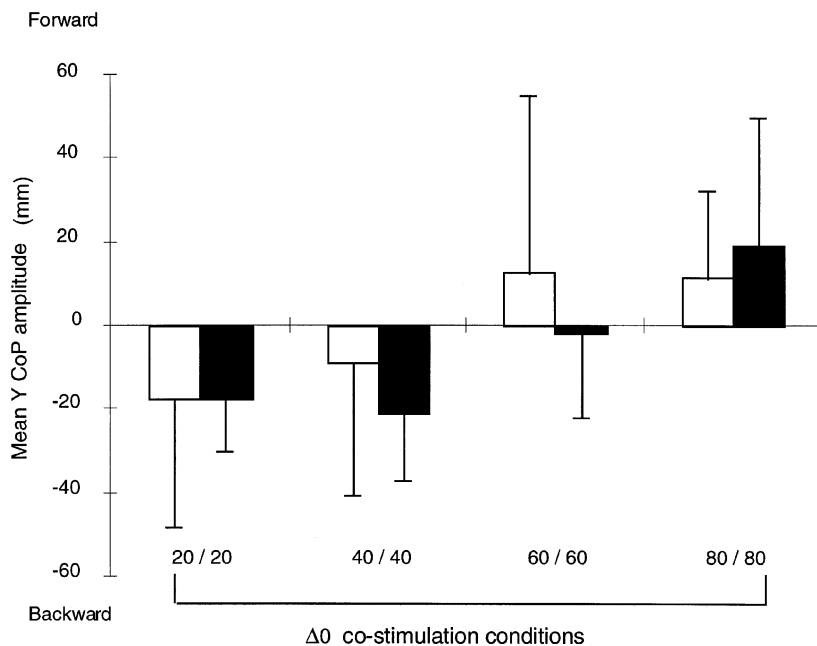
Figure 4. Mean postural responses induced by combined proprioceptive and tactile stimulation at the same frequency (20, 40, 60 or 80 Hz)

□, mean experimental amplitudes of the Y CoP displacements obtained under all the Δ0 co-stimulation conditions. ■, expected mean values resulting from the theoretical sums of the isolated effects induced by vibrating separately the two sensory channels. Note that no significant differences were found between the experimental and theoretical values.

respectively applied to the foot soles and ankle muscles, that is when the levels of the afferent activation were low. Conversely, when the frequency difference was in favour of the proprioceptive stimulation, the greater proprioceptive effect was observed in response to the higher level of sensory co-activation (Fig. 6).

As with the Δ0 frequency conditions, no significant differences were found between the mean experimental amplitudes of the Y CoP displacements induced under all the co-vibration conditions at different frequencies and

the theoretical amplitudes obtained by summing the isolated effects (Student's paired t tests, $P > 0.05$; Fig. 6).

Taken together, the results show that the co-activation of proprioceptive and tactile modalities gave rise to specific oriented whole-body tilts whose direction and amplitude clearly depended on both the frequency difference and the absolute levels of vibration frequencies applied. In all cases, the postural responses corresponded to the sum of the effects obtained upon stimulating separately the two sensory modalities.
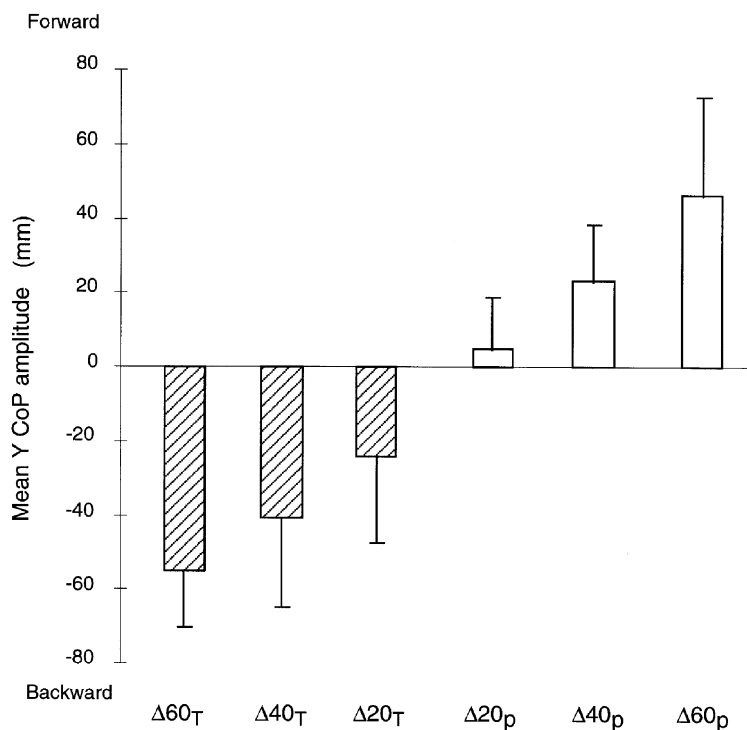

Figure 5. Mean postural responses induced by combined proprioceptive and tactile stimulation according to the difference in vibration frequency used

Each bar corresponds to the mean amplitude of the Y CoP displacements recorded for all the subjects under the various patterns with frequency differences of the same magnitude (Δ20, Δ40 or Δ60 Hz) in favour of the tactile (T) or the proprioceptive (P) stimulation.

DISCUSSION

Functional significance of the vibration-induced body tilts

Whatever the vibration frequency used, vibrating the two tibialis anterior muscles or the forefoot zones of both soles resulted in whole-body shifts with similar mechanical and EMG profiles but of opposite polarity. The body tilted forwards after proprioceptive stimulation and backwards in the case of tactile stimulation.

In both cases, early EMG responses in the tibialis anterior or soleus muscles seem partly responsible for the subsequent oriented postural responses because they caused either a plantar- or dorsiflexing ankle torque, which in turn might cause a large rotation of the body in the opposite direction. Similar motor responses have been described after vibratory stimulation was applied to either the soleus or the dorsal neck muscles (Eklund, 1972; Gregoric *et al.* 1978; Lekhel *et al.* 1997), or after a galvanic vestibular stimulation (Lund & Broberg, 1983; Fitzpatrick *et al.* 1994), or a moving visual scene (Bronstein & Buckwell, 1997).

The fact that ankle muscle responses are similar after separate manipulation of almost all sensory modalities and that their latencies are relatively long suggests that the resulting postural responses are not due only to local reflexes (Eklund, 1972; Hagbarth, 1973; Gurfinkel *et al.* 1976; Smetanin *et al.* 1993; Lekhel *et al.* 1997). Furthermore, the fact that not only the ankle muscles but also the thigh muscles were activated at the same time in response to galvanic vestibular stimulation supports this view (Iles & Pisini, 1992). In fact, what has been generally proposed is that more integrative mechanisms involving supraspinal structures might underlie the co-ordinated motor responses and the resulting whole-body displacements. The functional interpretation currently advanced is that the postural responses of proprioceptive origin might occur to compensate for a virtual body tilt simulated by a vibration whose direction would correspond to the lengthening of the vibrated ankle muscle (Roll *et al.* 1993; Hlavacka *et al.* 1996; Massion, 1998; Kavounoudias *et al.* 1999*a*). Similarly, the body tilts induced by plantar stimulation can also be interpreted as postural responses compensatory to a virtual body deviation for at least two reasons: (i) the whole-body tilts were always oriented contralaterally with respect to the stimulated plantar zone, (ii) skin mechanoreceptors are very sensitive to mechanical vibration, especially the slowly adaptive receptors, which are able to code every pressure change exerted on their receptive fields (Vedel & Roll, 1982). Therefore, applying vibration under a delimited plantar area probably simulates a local pressure increase, as when the body is actually tilted in the direction of this area.

Nevertheless, the question arises as to whether the foot sole vibration is actually selective. In particular, it cannot be ruled out that the vibration applied on the plantar forefoot zones would spread towards flexor foot muscles since the specific activation of these muscles would also give rise to a backwards postural response. However, as we have previously shown (Kavounoudias *et al.* 1998), stimulation of the forefoot zones together with the heels never evoked backward body tilts but only small body oscillations. Note also that a single flexor muscle activation cannot explain the laterally oriented body tilts
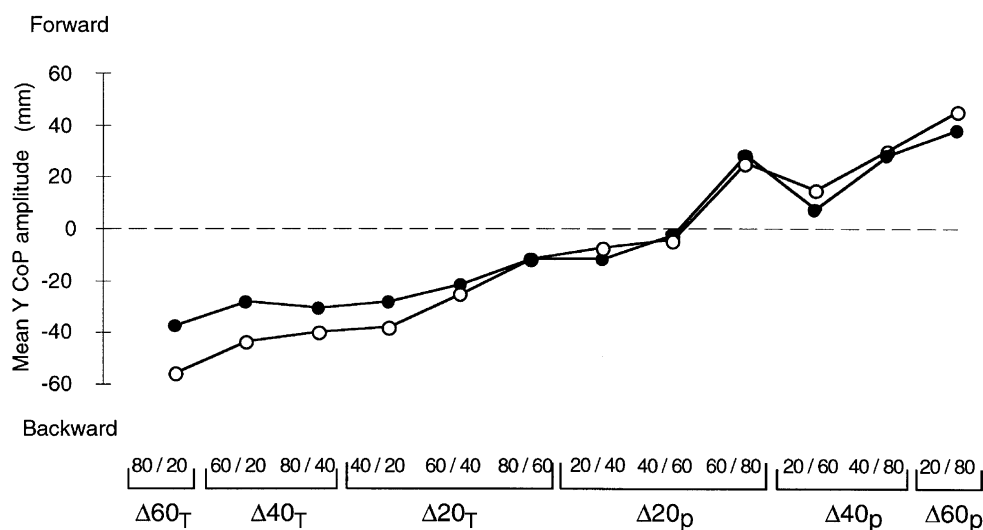

Figure 6. Comparisons between the mean experimental (○) and theoretical (●) amplitudes of the postural effects in response to different combined stimulation conditions

For each set of posturographic data, the co-vibration pattern is indicated by two frequency values, which correspond to the tactile and proprioceptive stimulations. Note that whatever the co-stimulation condition, no difference was found between the mean experimental and theoretical values.

observed after the stimulation of only one sole (Kavounoudias *et al.* 1998).

Furthermore, to verify that the responses were effectively plantar, in a preliminary study we investigated whether similar postural effects could be observed using low-intensity transcutaneous electrical stimulation (Meyerson, 1983) applied to the foot soles of five standing subjects. Under these conditions, the cutaneous sensation as well as the oriented postural responses induced by the electrical stimulation were similar to those obtained with vibration. As for vibratory stimulation (Kavounoudias *et al.* 1998), the body tilted backwards after stimulation of the forefoot plantar zones, forwards in the case of co-stimulation of the two heels, and laterally after the selective stimulation of only one foot sole (Fig. 7).

Therefore, the artificial sensory messages elicited by selectively activating proprioceptive as well as tactile afferents with vibratory stimulation induce specifically oriented postural responses aimed at reducing the gap with respect to the vertical posture. In addition, the fact

Figure 7. Oriented postural responses induced by transcutaneous electrical stimulation of the forefoot and/or heel zones of the soles

The plantar regions were stimulated by pairs of surface electrodes (●): delivery of rectangular pulses (0.5 ms duration, 100 Hz) at non-painful intensity (1.2× perception threshold). Individual final positions of the CoP after 2.5 s of stimulation for 5 subjects are shown (○); their means are represented (□). Vectors show that body tilts are contralaterally oriented with respect to the stimulation sites.

that the amplitude of the vibration-induced whole-body tilts was found to be linearly frequency dependent shows that skin and tendon vibration are suitable tools to simulate body deviation with a given amplitude. Microneurographic recordings have shown that muscle spindles as well as cutaneous mechanoreceptors respond to vibration following a one-to-one mode in the frequency range used in this experiment (Burke *et al.* 1976; Ribot-Ciscar *et al.* 1989; Roll *et al.* 1989).

A complementary contribution of proprioceptive and tactile information for stance regulation purposes?

The amplitude of the whole-body tilts induced by applying the same vibration frequency to the plantar forefoot zones or to the flexor ankle muscles was not found to be identical: in the low frequency range, tactile stimulation gave rise to more powerful postural effects than those elicited by proprioceptive stimulation; conversely, this tendency was reversed with stimulation at higher frequencies. Moreover, whatever the frequency used, the postural responses induced by vibrating the flexor ankle muscles always occurred later than those elicited upon vibrating the forefoot zones of the soles. Taken together, these findings suggest that tactile and proprioceptive afferents from soles and ankle muscles could subserve complementary functions for postural purposes: the regulation of small amplitude body sways would be predominantly assigned to tactile inputs, whereas ankle muscle proprioception would be mainly involved in the regulation of larger body sways.

Results from studies of human muscle spindle activity during normal standing bring further arguments in favour of this hypothesis (Aniss *et al.* 1990*a*,*b*). Recordings of Ia afferents from muscles of the anterior part of the leg in blindfolded standing subjects revealed a poorly sustained proprioceptive activity. Only 50% of afferents were spontaneously active and their mean discharge frequency never exceeded 4 Hz s⁻¹. According to these authors, slow and small amplitude movements in the antero-posterior plane generally produced very little neural afferent modulation whereas faster and greater body sways generated Ia activity in phase with the stretching phase (Aniss *et al.* 1990*b*). These data support our results, namely the idea that proprioceptive information from pretibial muscles has a poor aptitude to signal the small body oscillations around the vertical axis whereas these receptors would be massively activated by larger body displacements in the sagittal plane associated with muscle contractions necessary to restore balance. The regulation of slow range body movement would be preferentially controlled by cutaneous feedback from the soles, providing the CNS with the permanent small body changes with respect to the vertical posture, and by activating short latency and powerful postural reflex loops. This last proposition is consistent with data from Diener *et al.* (1984) showing that the exclusion of somatosensory afferents from the feet by means of an
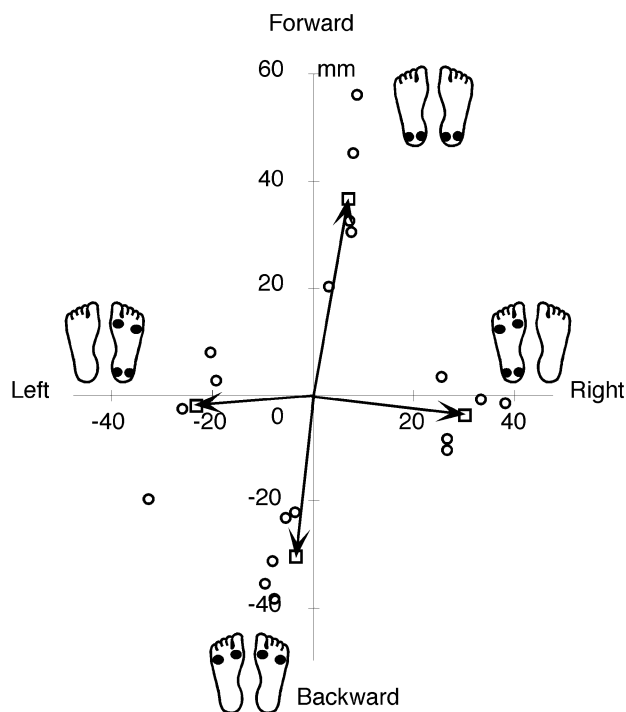
ischaemic block applied at the ankle level only affected regulative postural responses induced by small amplitude (4 deg) and low frequency (0.3 Hz) movement of the support.

An additive influence of proprioceptive and tactile information in postural regulation

Whatever the vibration frequency, additive postural responses were found upon co-stimulating the two forefoot zones of the soles and the two tibialis anterior muscles. A first interpretation would be that the system behaves as if there were independent competing responses. Although this hypothesis cannot be ruled out, a body of data argues in favour of an integrative mechanism of multiple sensory inputs for postural regulation (Horak & Macpherson, 1996; Mergner & Rosemeier, 1998). In particular, similar additive effects have already been described in response to combined vestibular and neck muscle stimulation in the case of postural control (Hlavacka *et al.* 1995, 1996) but also for perceptual purposes (Karnath *et al.* 1994). Therefore, one might expect that, in our experimental context, tactile and proprioceptive inputs would be co-processed following vector addition laws to jointly assure balance regulation. Such vectorial rules for the integrative processing of multiple sensory information might allow permanent assessment of the body position and its changes on the basis of the relative degree of congruence between several convergent inputs. In fact, the direction and the amplitude of the body tilts clearly depended on the difference between the vibration frequencies simultaneously applied to the forefoot zones and the ankle flexor muscles. Similar results from various studies focusing on only one sensory channel have shown, for instance, that co-vibrating two antagonist muscles at the same joint could give rise to perceptual or motor responses only when a difference in vibration frequency was introduced (Gilhodes *et al.* 1986; Calvin-Figuière *et al.* 1999; Kavounoudias *et al.* 1999*a*). Postural responses found in response to co-vibrations of the forefoot and heel zones of both soles also suggested that the relative distribution between the pressures exerted on these two plantar zones could efficiently indicate to the CNS the body position with respect to the vertical (Kavounoudias *et al.* 1999*b*).

Taken together, these data show that multiple sensory information arising from one or various sensory sources might be co-processed following a common vectorial-addition mode for postural regulation purposes. Such an integrative mechanism does not imply that the relative contributions of all sensory modalities have to be equivalent, however. Rather, this study suggests that proprioceptive and tactile feedback might be differentially involved in human postural control according to body or environmental constraints.

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Acknowledgements

Corresponding author

A. Kavounoudias: Laboratoire de Neurobiologie Humaine, UMR CNRS 6562, Faculté de Saint-Jérome, Case 362, 13397 Marseille cedex 20, France.

Email: anneka@up.univ-mrs.fr